Polyphagy in True Bugs: A case study of *Leptoglossus phyllopus* (L.) (Hemiptera, Heteroptera, Coreidae)[1]

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Abstract: The polyphagous species *Leptoglossus phyllopus* (L.) was examined with respect to host plant preference, tissue feeding specificity, seasonal dispersal among host plants, and life history. Mark-recapture, census, and rearing experiments demonstrated that this species exhibits true polyphagy, in that individual bugs feed on plants from more than one family. Developmental parameters such as growth and survivorship did not differ among plants from several families, but did vary significantly with quality of host (e.g., wild vs. cultivated). Stadium duration, however, varied among wild host plant species in laboratory experiments. Specialization on reproductive plant parts, coupled with sequential polyphagy and dispersal among a variety of seasonal host plants, allows multiple generations per year. Modes of feeding and preferred target tissues among coreids are discussed.

Key words: leaffooted bug, *Leptoglossus phyllopus*, polyphagy, stylet sheath, target tissue.

Introduction

For phytophagous insects with piercing-sucking mouthparts, feeding selectivity operates on two levels: preferred target tissue and host plant species. Tissue preference is considered to be a conservative evolutionary character (TONKYN & WHITCOMB 1987); for example, specialization on xylem, phloem, or parenchyma is characteristic of subfamilies or families in Auchenorrhyncha (PORT 1978). Phytophagous Heteroptera have been extensively analyzed with respect to several factors associated with target tissue preference: mouthpart morphology, salivary chemistry, preference for plant parts or structures, and mode of feeding (MILES 1972; COBBEN 1978; MILES & TAYLOR 1994; HORI 2000). The enzyme components of heteropteran saliva are considered to be a family-level character (MILES, cited in HORI 2000), although induction of proteolytic enzymes has been demonstrated in a zoophytophagous mirid (ZENG & COHEN 2001). The mode of feeding may also be associated with particular taxa. Mirids (e.g., *Lygus* spp.), for example, employ a macerate-and-flush process, whereas an osmotic pump mechanism is associated with coreids (MILES & TAYLOR 1994). However, some pentatomids and lygaeids shift between salivary sheath formation and lacerate-and-flush feeding (MILES 1972).

Preference for a particular plant developmental stage or structure (e.g., growing shoots, buds, ripe seeds), may also be associated with specific groups. Pyrrhocoroidea feed predominantly on mature seeds, tingids prefer mature leaves, while phytophagous mirids concentrate on flowers, buds, and new foliage (SCHUH & SLATER 1995). In some cases, however, such trends only become evident at the tribal or even generic level. SCHAEFER & MITCHELL (1983) noted that an affinity for vegetative or reproductive structures is characteristic of tribes within the Coreidae. Among Australian coreids, KUMAR (1966) recognized two different types of feeding – exclusive sap feeding is found in some genera whereas others feed on both sap and fruit. However, such

[1]Dedicated affectionately to Ernst Heiss, my delightful colleague on the Executive Committee of the International Heteropterists' Society and heteropterist extraordinaire.

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diversity of feeding was considered by COBBEN (1978) to indicate a "phase of unbalanced equilibrium."

Even fewer generalizations may be made regarding host-plant specificity. Curiously, the question of diet breadth in Heteroptera has not been explored with the intense fervor devoted to insect-plant interactions in Lepidoptera, Orthoptera, and other orders of chewing insects. COBBEN (1978) characterized the Tingidae as monophagous while suggesting that "polyphagy prevails" among the phytophagous Miridae; but he provided no comparable analysis for the Pentatomomorpha. Nearly 30 years have passed since the publication of COBBEN's (1978) monumental study of mouthparts and feeding strategies, but our understanding of heteropteran-plant relationships remains limited. Neither facultative zoophagy nor the extreme polyphagy associated with some heteropterans is properly understood (ZENG & COHEN 2001). WHEELER (2001) observes that despite an extensive literature on crop injury, there are "large gaps in our knowledge of mirid-plant interactions." Information for some heteropteran groups is lacking, detailed ecological studies of bugs outside of agroecosystems are uncommon, and adult host plant records are not always reliable indicators of breeding hosts (SCHAEFER & MITCHELL 1983).

Polyphagy in Heteroptera is of great interest from both an economic and an evolutionary standpoint. Many of the major agricultural pests (e.g., *Nezara viridula* (L.), *Riptortus clavatus* (THUNBERG), *Leptoglossus zonatus* (DALLAS), *Lygus lineolaris* (PALISOT DE BEAUVOIS)) have a wide range of host plants (SCHAEFER & PANIZZI 2000). However, it is important to distinguish between generalist species composed of more specialized populations and polyphagy at the individual level (i.e., diet mixing) (FOX & MORROW 1981; BERNAYS & MINKENBERG 1997). The evolution of omnivory has been shown to correlate with polyphagy in Heteroptera (EUBANKS et al. 2003), and these authors proposed that polyphagous, seed-feeding herbivores may be more likely to expand the diet to consume animal prey. COBBEN (1978, 1979) considered polyphagous carnivory to be plesiomorphic within Heteroptera. For phytophagous groups, he proposed that sap-feeding originated from polyphagous seed-feeding, with the former mode of feeding tending toward a more restricted host range (COBBEN 1978). In Hemiptera in general, tissue-feeding specialization has been associated with host plant specificity (BERNAYS & CHAPMAN 1993), but this observation is based primarily on the British fauna, and is biased toward Sternorrhyncha and Auchenorrhyncha. Clearly, more information on polyphagy in Heteroptera is needed.

The objective of this research was to conduct a detailed study of polyphagous feeding behavior in a single coreid species, the leaffooted bug *Leptoglossus phyllopus* (L.). Host range and dispersal, seasonal patterns of host plant use, preferred feeding site, and target tissue were examined in order to characterize the factors influencing host plant selection. *Leptoglossus phyllopus* damages legumes, tomatoes, tree nuts, and citrus in the southern and eastern United States (MITCHELL 2000), and is considered a minor economic pest. The primarily Neotropical genus *Leptoglossus* GUERIN was selected for study because it includes species exhibiting widely disparate feeding strategies ranging from strict monophagy to extreme polyphagy, as well as a number of species of economic importance. Several *Leptoglossus* species are presently expanding their ranges – and potential for economic damage – geographically. The highly polyphagous *L. zonatus* (DALLAS), a pest of many crops in Mexico and South America, has recently invaded the southeastern United States to Florida (BUSS et al. 2005) and has become a pest of Satsuma oranges in Louisiana, displacing *L. phyllopus* (HENNE et al. 2003). *Leptoglossus occidentalis* HEIDEMANN, once restricted to conifers in western North America, has spread rapidly eastward across the continent to Ontario and New England (RIDGE-O'CONNOR 2001). Accidentally introduced into Italy in 1999 (TAYLOR et al. 2001), this species has now spread to Central Europe (RABITSCH & HEISS 2005). Thus, information on the feeding behavior of *L. phyllopus* may be applicable not only in the southeastern United States, but to congeneric species of economic importance elsewhere.

Materials and Methods

Study site: Research was conducted primarily at Brackenridge Field Laboratory (BFL), operated by The University of Texas at Austin. This field station is located inside the city limits of Austin, Texas, along the shores of the Colorado River, and comprises 32 hectares of grassland, cedar-post oak scrub and semi-deciduous woodland.

Four study plots, each measuring 92.9 m^2, were established at BFL to investigate seasonal activity of *L. phyllopus* and other coreids. All plots were located in either early successional or cultivated garden areas. Plot 1, on the river terrace, was dominated by Johnsongrass, *Sorghum halepense* (L.) PERS., and various composite species. Plot 2, bordering an artificial pond, was composed primarily of grasses and composites interspersed with prickly pear (*Opuntia* spp.) and mesquite (*Prosopis glandulosa* TORR.). The remaining study plots were placed in the cultivated garden area to ensure an adequate water supply during summer drought. Plot 3, formerly under cultivation, had returned to native early successional vegetation two years before the commencement of research. Plot 4, the agricultural study plot, was planted each spring with tomato (*Lycopersicon esculentum* P. MILL.), giant sunflower (*Helianthus annuus* L.), and okra (*Hibiscus* [=*Abelmoschus*] *esculentus* L.). A sprinkler system provided water for both garden plots twice weekly, and fertilizer was applied to cultivated plants according to standard agronomic practices.

Field census: From July to November 1977, and February to November 1978, *L. phyllopus* individuals were visually counted in each study plot at weekly intervals. All censuses were taken within two hours of sunset, a time of maximal copulation and feeding activity. Field work was discontinued during the winter (mid-November through mid-February), as no bugs were active during this period. For each individual observed, the following data were collected: location on plant (leaf, stem, bud, etc.), plant species and reproductive condition, instar (nymphs), and copulatory activity (adults).

From March to June 1979, a modified bug census was conducted weekly in Plot 1. Both *L. phyllopus* and another coreid, *Euthochtha galeator* (F.), were monitored. Number of adults, nymphs of all instars, and copulations were counted. Location of bugs on the plant was noted in greater detail than in earlier censuses, differentiating between bud, stem, and leaf primordia as well as between mature plant organs. The 1979 census covered the entire reproductive life span of the host plant *Cirsium texanum* BUCKL., from bolting through seed set.

A plant census was conducted monthly in each study site in conjunction with the bug censuses in 1977 and 1978. Each plot was subdivided into 40 equal quadrats, and a wire square measuring 930 cm^2 was tossed twice into each quadrat. This quadrat method was designed to eliminate the unequal representation of marginal areas frequently associated with sampling by random toss (SOUTHWOOD 1966). After each throw, presence or absence of plant species within the wire sampler was noted, in order to compute frequency of occurrence from a total of 80 samples per study plot. Additionally, counts were taken of number of stems, buds, flowers, developing fruits, and mature fruits of host plants within the confines of the wire square. All counts were made visually in the field, and no plant material was removed from the study areas. All *Leptoglossus* host plants were identified to species. With the exception of grasses, non-hosts were identified at least to genus. Within the Poaceae only *S. halepense* was distinguished; other grasses were lumped in a single category. Plant family designations follow JUDD et al. (2002); species and describer names follow RADFORD et al. (1968) and CORRELL & JOHNSTON (1970). In 1979, only host plants were surveyed. Finer distinctions were used in the census of plant structural and reproductive organs, to correspond with the more detailed bug distribution studies.

For statistical analysis, plants were categorized as reproductive or non-reproductive, and bug counts ($\log_{10}$ bug density for each non-zero census date) were correlated with density of reproductive plants for *C. texanum* in Plot 1 and *Heterotheca latifolia* BUCKL. in Plots 2 and 3.

Mark-recapture: Mark-release-recapture studies were carried out at BFL from

Fig. 1: *Leptoglossus phyllopus* adults; clockwise from upper left: aggregated on *Cirsium* sp., March, Brazos Co., Texas (Photo: W. O. Ree Jr.); in copula on *Gaura parviflora*, July, Burleson Co., Texas (Photo: A. Calixto); aggregated with marked bug on *Helianthus annuus*, August, Travis Co., Texas; feeding on *Solidago* sp., October, Brazos Co., Texas (Photo: W. O. Ree Jr.); feeding on *G. parviflora*, July, Burleson Co., Texas (Photo: A. Calixto).

June 1976 through November 1977. Adult *L. phyllopus* were individually marked by painting the pronotum with typewriter correction fluid (Liquid Paper™) and numbering with india ink (Fig. 1). A total of 1,070 individuals was marked during the course of the study. Bugs were collected in the field by dropping net bags over aggregations on host plants, and were returned to the laboratory for marking. With rare exceptions, each batch was completed and released on the date of capture. Bags of marked individuals were attached to a branch or stem of the original host plant and opened, allowing bugs to emerge. The effect of prominent white dorsal markings on bugs in the field is unknown, but this technique does not significantly alter survivorship or copulatory activity of individuals under laboratory conditions (Mitchell unpubl. data). Mark-release-recapture studies were designed to examine dispersal, host plant shifts, and length of residency, rather than population size. Consequently, initial marking was a discontinuous process, although study areas were checked daily or twice daily for recaptures. Thirteen subsites (host plant patches) were delineated in the mark-release-recapture

study. Size of subsites was variable, being a function of host plant density in a given area, and ranged from a single *Callicarpa americana* L. bush to a 30 m^2 stand of *H. latifolia*. Distance between subsites was measured from center to center of each patch. Analysis of dispersal therefore did not account for movement within the larger subsites, and total movement may have been slightly underestimated. Each subsite was characterized by one dominant host plant species.

The following data were collected for each marked individual: sex, subsite, time of collection, host plant species, absence of legs, presence (and position) of macrotype tachinid eggs on exoskeleton, degree of sclerotization (teneral vs. mature) and wing wear condition (tattered vs. whole). Beginning in August 1976, bug length was measured with calipers to the nearest 0.5 mm. At each subsequent recapture original observations were rechecked, with the exception of length measurement. Further information collected for resighted individuals included location on host plant and activity (e.g., sitting, walking, probing, sucking, copulating).

Data from the pilot study (June to September 1976) and overwintering periods (October to February of both years) were analyzed separately from the major mark-release-recapture project in 1977. Marking of the overwintering generation proved unsuccessful; no bugs marked in late fall of either year were ever sighted again the following spring. Pilot project data were analyzed by hand to determine host plant and subsite shifts by individual bugs.

The mark-release-recapture project in 1977 involved a total of 543 individuals and three complete generations of *L. phyllopus*. Bugs were separated into four generational categories (overwintering, spring, summer, fall) on the basis of wing wear and sclerotization. Data were processed using the LONGPOP program (WATT et al. 1977, 1979). This program applies the capture-recapture methods of JOLLY (1965) for calculation of survivorship, and also tabulates dispersal and other population parameters. Sex ratios were tested using χ^2 goodness-of-fit (ZAR 1999).

Colony maintenance: *Leptoglossus phyllopus* colonies were reared at 26 ± 2°C, and a photoperiod of 16:8 [L:D], and were fed whole green beans, *Phaseolus vulgaris* L. and shelled organically grown sunflower (*H. annuus*) seed. Adults were housed in screen and Plexiglas™ cages (25 x 25 x 25 cm) provided with wooden applicator sticks for oviposition. Nymphs were maintained in smaller cages constructed from 300 ml plastic drinking cups (cup cages) and provided with a constant source of water through cotton dental wicks.

Rearing experiments: Conducted in both laboratory and field, these experiments examined the ability of fifth-instar *L. phyllopus* to develop on a variety of hosts from different plant families at different stages of development. Three variables were used to measure host plant suitability: duration of the fifth instar, growth increment during this period, and survivorship. Experimental bugs were derived from field collected parents, and were reared in the laboratory. Rearing colony cages were checked nightly, at growth chamber sunset. All newly molted fifth instars were collected at this time, isolated in screen-covered cups overnight, and supplied with a green bean for moisture. Distribution of nymphs among treatments was completed within 24 hours. Assignment to treatment was randomized within the set of host plants in the appropriate developmental condition at a given point in time.

Each nymph was measured with calipers to the nearest 0.5 mm before placement on the experimental host plant. Cages were checked daily at sunset, and newly molted adults were re-measured. Growth increment was calculated as the difference between these two length measurements. Instar duration was defined as days elapsed between the fifth instar and adult molts. Survivorship, assessed only in laboratory experiments, was calculated as number of surviving nymphs per cage.

In the laboratory, detached fruits or seed heads of a single plant species were offered as a food source. Each experimental cup cage contained five bugs, individually marked with enamel dots on the tibial foliation. Laboratory experiments involved six treatments, consisting of laboratory diet

control and five host plants: *Callicarpa americana* L. var. *lactea* (Lamiaceae), *Campsis radicans* (L.) SEEM. (Bignoniaceae), *Gaura parviflora* DOUGL. (Onagraceae), and *Solanum eleagnifolium* CAV. (Solanaceae). Each treatment consisted of four cages for a total of 20 nymphs per treatment.

In field experiments, bugs were caged individually on live host plants (n = 25). Tulle sleeves, measuring 45 by 25 cm, were lowered around plant stems or branches, and fastened at the base with fine wire. Vegetative portions of the plant, flower buds, or one or more developing seed heads (depending on the growth form of the plant) were contained within each sleeve cage. After addition of a nymph, each sleeve was wired together at the top, enclosing both bug and plant. Plants were maintained in the bud stage by clipping flowers within the cage as they opened, or moving the entire cage to a new plant. Field experiments concentrated mainly on species in the family Asteraceae. Treatments included *Baccharis neglecta* BRITT. (Astereae), *C. texanum* (Cynareae), *Gutierrezia texana* (DC) TORR. & GRAY (Astereae), *H. annuus* (Heliantheae), *H. latifolia* (Astereae), *Solidago altissima* L. (Astereae), and *G. parviflora* (Onagraceae). The last four species were tested in all three developmental stages; other hosts listed were tested only in reproductive condition.

Field experiments were conducted from September to November of 1977, and May through July of 1978, according to the phenology of host plants studied. Separating the influence of climatic variation from genuine treatment effects was therefore critical. A series of controls was established, in order to monitor the combined effects of temperature and daylength and also laboratory stock quality. In the laboratory control treatment, bugs received standard rearing diet (beans, sunflower seeds and distilled water), and were maintained in the growth chamber at 16:8 [L:D] photoperiod conditions. Additionally, tulle cages supplied with laboratory diet were set up on the roof of the Zoology building on the University of Texas campus. One set of these "roof controls" was conducted in fall of 1977, and one in summer of 1978.

Field data from mark-recapture studies were also analyzed to substantiate the experimental results for fifth instar growth increment. Adult length of *L. phyllopus* marked as teneral individuals was compared among various host plants. Adult length of males and females was analyzed separately for these data, because sex ratios were not equivalent across treatments.

Measurement data from both field and laboratory experiments were analyzed by t tests or by one way analyses of variance (ANOVA) followed by Fisher's LSD. Logarithmic (base-10) transformation was used prior to ANOVA if needed to normalize data or correct for unequal variance (MINITAB 2000). Count data were analyzed by nonparametric tests, including Friedman two-way ANOVA, Kruskal-Wallis (MINITAB 2000), and non-parametric rank analog of Tukey's test (CONOVER 1971).

Laboratory choice tests: Choice experiments were conducted in small cup cages. Naive second instars were used in all tests. Field observations identified this instar as the first critical period of host plant selection, because the previous instar is a non-feeding stage, and oviposition site does not necessarily reflect host plant preference (MITCHELL & MITCHELL 1986). Nymphs used in experiments were derived from field-collected adults, but reared from the egg stage in the laboratory. Prior to placement in testing cages, bugs received only green bean (a water source), and were not exposed to laboratory diet.

Since early instar nymphs are normally gregarious, bugs were tested in groups of five per cage. Preference between plant species was tested by offering seed heads of *H. latifolia* (Asteraceae) and *G. parviflora* (Onagraceae) as alternative food choices; preference for plant parts was tested using buds and immature seed heads of *C. texanum*. For each comparison, 36 replicates were conducted, using a total of 180 second instars. Each testing cage contained one cut stalk (ca. 8 cm) of each plant alternative, inserted in separate water vials. Fresh plant cuttings for each experiment were collected daily at the field station. Following addition of nymphs, cages were observed at 4-h intervals during the 16-h growth chamber day,

and again at sunrise of the following day. Stylet insertion was considered to represent definitive choice. A single observation, that which involved the greatest number of feeding individuals, was selected from each experimental data set. A sign test (ZAR 1999) was performed on the resulting values.

Histology: Plant tissue exposed to heteropteran feeding was sectioned and examined under a light microscope. Field collected plant material was supplemented by caging bugs on potted plants and cuttings in the laboratory. Sites of observed stylet insertion were marked on the plant surface with an indelible pen. Marked plant tissue was cut with a single edge razor blade, allowing a margin of ca. 2 mm. around the point of insertion, and fixed in either Carnoys solution (0.5 hr) or formalin-acetic acid-alcohol (FAA) (48 hrs). Material fixed in Carnoys was dehydrated through a series of ethyl alcohols to xylene, while FAA treated tissue was dehydrated with tertiary butyl alcohol, following the method of JOHANSEN (1940). Although both procedures were satisfactory, that of Johansen proved more consistently reliable. Dehydrated tissue was embedded in Paraplast™ and sectioned at 15 microns on a rotary microtome. Serial sections obtained in this manner were rehydrated and stained with a 1 % solution of safranin in 50 % ethanol, and counterstained with fast green (0.2 % in 50 % ethanol). Best results were obtained using a staining schedule of 2 h in safranin solution, followed by 1 min in fast green and 2 min in each of two 95 % alcohol baths.

After staining and subsequent dehydration of sections, coverslips were mounted with Permount™. Bug salivary sheaths stain bright pink with safranin. Xylem stains red in contrast to the fast green absorbed by parenchyma and other non-lignified plant tissues. Both stylet tracks and damaged plant tissue were easily observed using this staining technique. As the plane of sectioning only rarely coincided with the path of insertion, seriality of sections was critical in determining the termination point of the stylet tracks. Rare sections bearing complete, parallel-cut salivary sheaths were photographed at 100x with a Nikon Eclipse E600 microscope equipped with an Olympus DP10 digital camera.

Stylet tracks of *L. phyllopus* were examined on the wild host *C. texanum*, and also on cultivated green cherry tomato (*L. esculentum*), and green bean (*P. vulgaris*). In addition, feeding by the coreid *E. galeator* on *C. texanum* was investigated, as these two species coexist on thistle in the spring.

Voucher specimens: Specimens of the dipteran parasitoid *Trichopoda pennipes* F. are deposited in the California Academy of Sciences, Department of Entomology. Coreid specimens are in the insect collection at Texas A&M University, Department of Entomology.

Results

Field census. Although a diverse array of plants from seven families served as *L. phyllopus* breeding hosts at BFL (Table 1), plant species were not used in direct proportion to frequency of occurrence. One species in each study plot was always colonized to a greater extent than predicted on the basis of abundance alone, and others (e.g., grasses) were never used as breeding hosts at all. Temporal patterns of bug distribution on various wild and cultivated host plants are shown in Figure 2. Small vertical arrows indicate the beginning of plant reproductive activity. On thistle, tomato, sunflower and goldenrod, bug density increased dramatically following the transition from vegetative to reproductive growth. Colonization was concurrent with fruiting in the latter

Table 1: Nymphal host plants of *L. phyllopus*, Travis County, Texas, 1977-1979. Asterisk indicates observations at locations other than Brackenridge Field Station.

Plant family	Plant species	Common name
Asteraceae	*Achillea millefolium* L.	yarrow
	Baccharis neglecta BRITT.	desert willow
	Cirsium texanum BUCKL.	Texas thistle
	Gutierrezia texana (DC) TORR. & GRAY	broomweed
	Helianthus annuus L.	sunflower
	Heterotheca latifolia BUCKL.	camphor weed
	Solidago altissima L.	goldenrod
Bignoniaceae	*Campsis radicans* (L.) SEEM.	trumpet creeper*
Cucurbitaceae	*Cucurbita pepo* L.	squash
Lamiaceae	*Callicarpa americana* L.	French mulberry
Malvaceae	*Hibiscus* (=*Abelmoschus*) *esculentus* L.	okra
Onagraceae	*Gaura parviflora* DOUGL.	lizard-tail
Orobanchaceae	*Agalinis heterophylla* (NUTT.) SMALL EX BRITT.	prairie false foxglove
	Agalinis strictifolia (BENTH.) PENNELL	stiffleaf false foxglove
Scrophulariaceae	*Verbascum thapsus* L.	woolly mullein*
Solanaceae	*Lycopersicon esculentum* MILLER	tomato
	Solanum eleagnifolium CAV.	silver-leaf nightshade

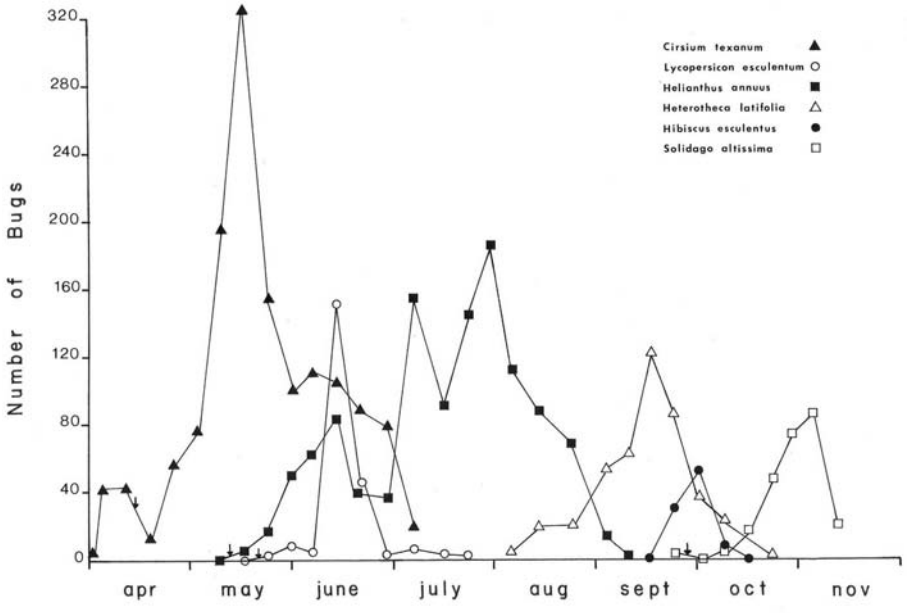


Fig. 2: Temporal patterns of *L. phyllopus* distribution on various cultivated and wild host plants based on 1978 census counts, Travis Co., Texas.

three species. Individuals dispersed between host plants with overlapping life cycles, as one host reached senescence and the next species began fruiting. Okra and *H. latifolia* become reproductive several months before bug invasion, but were never colonized during the vegetative stage. For a given plant species, bug density corresponded closely with abundance of plants in reproductive condition. The number of reproductive plants was significantly correlated with the log of bug density in the study area for both *C. texanum* ($r = 0.927$, $n = 15$, $P < 0.01$) and *H. latifolia* ($r = 0.692$, $n = 44$, $P < 0.01$); other plant species were not numerous enough for statistical analysis.

Leaffooted bugs were active from early spring to late fall, and overwintered as adults. Spring emergence varied from mid-February to late March, depending on the harshness of the winter. For 1976-1978, good correspondence was apparent between bug emergence and the condition of *C. texanum*, the first breeding host. In early spring, while thistles remained in the rosette stage, an occasional leaffooted bug could be observed probing on *B. neglecta*, a woody, late fall host. However, large aggregations of emerging adults did not appear in spring until thistles commenced bolting and produced the first central bud primordia. Copulation began 1-3 weeks after emergence from overwintering, and production of nymphs coincided with flowering and seed development of *C. texanum*. Nymphs hatched prior to flowering only in 1979, and buds were used temporarily as a food resource until developing seed heads became available.

Preference among plant reproductive structures is best documented by the detailed data for *C. texanum* in spring of 1979 (Fig. 3). Weekly plant censuses and biweekly bug counts covered the period from appearance of the first bud primordia in April until seed set in early June. For each census date, numerical tallies were converted to percentages, to facilitate comparisons between plant organ availability and bug utilization. Percent bug utilization was calculated as number of bugs on a given plant structure (e.g. bud, flower, etc.) divided by total bugs observed on reproductive organs of that host plant species. Plant percentage values were determined in a similar manner. Preference was indicated when bug percentage use exceeded plant percentage availability. Total daily bug counts during the census ranged from 10 to 122; plant parts counted in each census ranged from 40 at first appearance of primordia to 302 at peak growth.

Early in the season, bugs concentrated on primordia (Fig. 3a), areas of the plant exhibiting rapid growth. As true buds appeared (Fig. 3b), abrupt switching behavior was evident, leading to disproportionately lower use of the still common primordia. Identical switching behavior accompanied the first appearance of developing seed heads (Fig. 3d), which continued as the preferred feeding site for the remainder of the season. Flowers (Fig. 3c), occurring during the same time period as immature seed heads, were rarely used. Ripening of seed heads in mid-June was not accompanied by an increased proportion of bugs on mature heads (Fig. 3e).

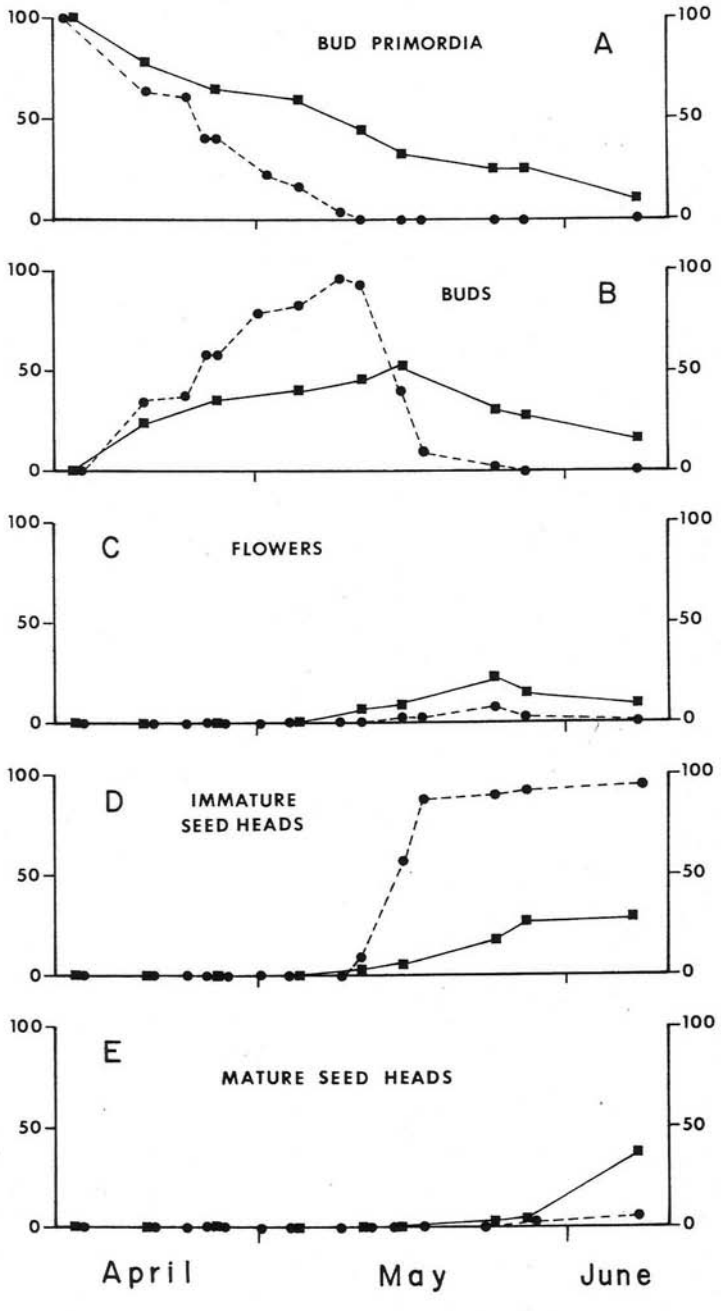
Similar census data for 1978 (not presented) also indicated an overwhelming preference for immature fruit and developing seed heads, and concomitant avoidance of open flowers and mature fruits and seeds; this was observed for *C. texanum*, *C. americana*, *H. latifolia*, and *S. altissima* consistently and for *H. annuus* in early season (June). Mature seed heads of the last species were preferred in July, and all seed heads were

used in proportion to abundance at the end of the season in August.

A comparison of *L. phyllopus* distribution with that of a less common coreid, *E. galeator*, on the same host plant shows a clear difference in utilization of plant parts of *C. texanum* (Fig. 4). Significantly higher numbers of *L. phyllopus* are found on reproductive structures (buds, flowers, and seed heads) compared with leaves or stems ($T = 8.22$, $df = 2$, $P = 0.016$), whereas significantly more *E. galeator* are found on stems (includes branches, petioles, and peduncles) than on leaves or reproductive parts ($T = 9.39$, $df = 2$, $P < 0.01$).

Mark-recapture. Analysis of 1977 capture-recapture data provided information on dispersal, longevity, copulatory activity, sex ratio, predation, and parasitism of adults, in addition to the primary objective of documenting individual host plant shifts. For males, 116 individuals were recaptured out of 300 marked (38.7 %); in total, 299 recapture events resulted in an average recapture frequency of 2.58. Of 243 females marked, 86 (35.4 %) were recaptured in 153 recapture events, for an average recapture frequency of 1.78. Females showed a greater tendency to disperse, although distance traveled was equivalent between the sexes; 31 female dispersants (36 %) moved an average of 42.31 m, whereas for the 33 male dispersants (28.5 %), the mean distance moved by dispersing individuals was 44.01 m.

The majority of individuals recaptured (71.5 % of males, 63.9 % of females) remained in a single patch of host plants. Most dispersants were recorded moving between separate patches of the same host plant species. However, multiple host shifts were documented. Teneral adults marked on *C. texanum* were subsequently recaptured while feeding on *H. annuus* (n = 4) and *L. esculentum* (7). One mature, fully sclerotized adult marked on *G. parviflora* was recaptured feeding on *H. annuus*. Mature individuals marked on *H. annuus* were observed feeding on *H. latifolia* (2), *L. esculentum* (1), and *Zea mays* L. (3). Marked individuals from *H. latifolia* fed upon *G. parviflora* (1), and *H. annuus* (4), while those from *L. esculentum* dispersed to feed upon *H. annuus* (8). The maximal number of host shifts observed was four per marked adult.



Marked bugs were also observed in copula. Among male *L. phyllopus*, eight bugs were observed to be mating on two separate occasions. One marked individual engaged in four copulations on different days. For females, three individuals were seen mating twice, and two engaged in copulations at least three times during the course of the study. Since subsites were checked only briefly each day (ca. 10 minutes per site), these observations represent only a small fraction of total copulatory activity. Caged bugs in the laboratory mated nearly every evening. No individuals marked as teneral

Fig. 3: Floral and fruiting stages of *Cirsium texanum*, Travis Co. Texas, April-June 1979, showing frequency of occurrence of each structure and distribution of *L. phyllopus*; squares connected by solid lines indicate percent occurrence of plant structure; circles connected by dotted lines indicate percent bug distribution on a structure.

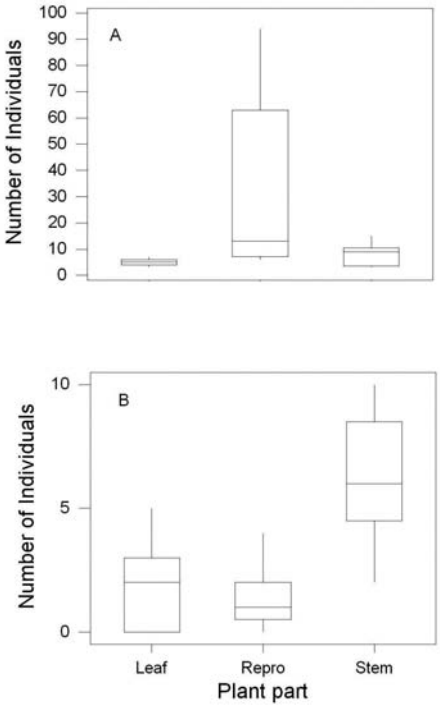


Fig. 4: Distribution of *Leptoglossus phyllopus* (**A**) and *Euthochtha galeator* (**B**) on leaves, stems, and reproductive parts of the host plant *Cirsium texanum*, Travis Co., Texas, April-May, 1979. Median value, first and third quartiles, and upper and lower ranges indicated by box and whisker plot.

adults were observed in copula on *C. texanum*, but four of the 11 dispersants sighted again on sunflower and tomato mated at least once on the adult host plant. After bugs reached adulthood, average residence time on the nymphal host plant (*C. texanum*) was 3.8 ± 2.1 days for males (n = 18), and 3.5 ± 2.1 days for females (n = 11).

Field longevity (e.g., residence rate) was slightly higher for males, and the longest interval between initial marking and final recapture was 51 days, as opposed to 42 for females. The recapture duration decay plot over time indicated a Type II survivorship pattern for both sexes. For males, the regression line may be expressed as y = 4.55 - 0.0878x, where x = days in residence and y = ln number of individuals (F = 1728.3; df = 1, 49; P < 0.005). For females, y = 3.94 - 0.0985x (F = 803.1; df = 1,40; P < 0.005).

Only the sex ratio of the overwintering generation on *C. texanum* was significantly biased toward males (s.r. = 0.602, n = 103, χ^2 = 4.28, df = 1, P < 0.05). Census data for 1978 corroborated this result (s.r. = 0.597, n = 613, χ^2 = 23.1, df = 1, P < 0.01). For five weeks following the initial colonization of the first spring host, males predominated; after this time and throughout subsequent generations, the ratio of males to females did not differ significantly from 1:1.

The large hind leaf-feet of bugs in the coreine tribe Anisoscelini detach easily, and may operate as a predator escape mechanism. The relative extent of predation in different populations may be estimated by frequency of leg loss, in much the same way that tail break frequency is used to compare predation rates among lizard populations (e.g., PIANKA 1970). Leg loss data for individuals collected during the capture-recapture study showed that only the overwintering generation on *C. texanum* exhibited a high rate of leg loss: 65 % of individuals remained intact (n = 100). In all subsequent generations, the percentage of undamaged individuals was considerably higher, ranging from 87.0-90.3 % (n ≥ 93). Summation of hind, mid, and foreleg loss frequency over the entire season yields 55 individuals lacking at least one hind leg, 41 lacking a middle leg and 13 with a detached foreleg. Although the foliated hind legs are lost somewhat more frequently than legs with simple tibiae, this trend may indicate only that predators preferentially approach from the rear, or that the expanded leaf-feet present a larger target for attack. Larger sample sizes would be required to verify a predator escape function for the tibial expansions.

A major natural enemy of *L. phyllopus* at BFL is the tachinid fly *Trichopoda pennipes* F. This parasitoid species (actually a complex of cryptic species or biotypes) is an important natural enemy of the economic pest *N. viridula* (JONES 1988), and leaffooted bugs serve as an alternative host in many crops in the southeastern United States (TILLMAN 2006). Other coreid genera attacked include *Acanthocephala*, *Anasa*, *Archimerus*, *Chelinidea*, *Euthochtha*, *Leptoglossus*, and *Narnia* (ARNAUD 1978). At BFL, *T. pennipes* has been reared from *Acanthocephala declivis* SAY, *A. femorata* (F.), *A. terminalis* (DALLAS), *Chelinidea vittiger* UHLER, and *Leptoglossus oppositus* (SAY) as well as *L. phyllopus* (Mitchell unpublished).

Intensity of parasitism was estimated as the proportion of adult bugs bearing a macrotype egg (or eggs) on the exoskeleton. Mark-recapture data indicated that high levels of parasitism were attained only in the overwintering and first spring generations, with 46 % and 27 % egg-bearing individuals, respectively. *Leptoglossus phyllopus* is the first hemipteran species to reach appreciably high densities in the spring, whereas alternate hosts (e.g., *A. femorata*, *Anasa tristis* (DE GEER), various pentatomid species) become common on garden crops somewhat later in the season. According to both mark-recapture and census data, <10 % of *L. phyllopus* in summer and fall populations bear tachinid eggs.

Oviposition site on the bug exoskeleton varies, but most eggs are placed on the head of *L. phyllopus*. Of 142 eggs examined, distribution on the body was as follows: head, 72.5 %; pronotum, 13.4 %; elsewhere on thorax, 9.9 %; abdominal sternites, 2.1 %; abdominal tergites, 0.0 %; tibial foliation, 0.7 %; wing, 1.4 %. The presence of a tachinid egg on the exoskeleton does not appear to deter an ovipositing *T. pennipes*. Occurrence of supernumerary *T. pennipes* eggs, although infrequent in females, was com-

Table 2: Development of fifth-instar *L. phyllopus* caged on various reproductive host plants in the field, Austin, Texas, Sept.-Nov. 1977 and May-July 1978.

Plant Species	Family	Season	n	Growth increment[a] (mm)	n	Stadium duration[a] (days)
Baccharis neglecta	Asteraceae	1977	10	4.15 ± 0.63a	10	15.10 ± 5.92a
Gutierrezia texana	Asteraceae	1977	13	4.00 ± 0.54a	13	14.69 ± 6.51a
Heterotheca latifolia	Asteraceae	1977	10	3.85 ± 1.16a	12	13.67 ± 7.57a
Solidago altissima	Asteraceae	1977	11	3.95 ± 0.65a	11	15.55 ± 6.39a
control[b]	——-	1977	6	4.33 ± 0.41a	10	11.20 ± 3.71a
Cirsium texanum	Asteraceae	1978	6	3.17 ± 1.13A	7	13.00 ± 3.61A
Gaura parviflora	Onagraceae	1978	10	3.45 ± 0.72A	10	13.30 ± 4.24A
Helianthus annuus	Asteraceae	1978	12	4.25 ± 0.75B	12	12.17 ± 2.85AB
control[b]	——-	1978	14	4.25 ± 0.85B	14	9.79 ± 2.04B

[a]mean ± standard deviation; within a season, means followed by the same letter do not differ significantly (ANOVA and Fisher's LSD test, P > 0.05); 1977: growth, F = 0.51; df = 4, 49; P = 0.728; instar duration, F = 1.09; df = 4, 55; P = 0.373; 1978: growth, F = 4.00; df = 3,41; P = 0.014; instar duration, F = 3.08; df = 3, 42; P = 0.039.
[b]control treatments were reared outdoors but received laboratory rearing diet

Table 3: Body length (mm) of teneral *L. phyllopus* collected from various nymphal host plants, Austin, Texas 1976-1977.

Host plant	Family	Season[a]	n	Males[b]	n	Females[b]
Baccharis neglecta	Asteraceae	F	14	15.86 ± 0.95a	—	——-
Gutierrezia texana	Asteraceae	F	—	——-	11	16.77 ± 0.52a
Heterotheca latifolia	Asteraceae	F	31	15.53 ± 0.87a	42	16.40 ± 0.76a
Solidago altissima	Asteraceae	F	28	15.75 ± 0.65a	15	16.83 ± 0.67a
Cirsium texanum	Asteraceae	S	58	15.55 ± 1.09A	46	17.23 ± 1.09A
Helianthus annuus	Asteraceae	S	27	16.24 ± 1.20B	27	17.87 ± 1.24B
Lycopersicon esculentum	Solanaceae	S	13	16.81 ± 1.07B	17	18.38 ± 1.15B

[a]F = fall hosts; S = spring/summer hosts; plants with collection sample size <5 not included.
[b]Mean plus standard deviation. Within a season, values followed by the same letter do not differ significantly (ANOVA and Fisher's LSD test; P > 0.05); fall: males, F = 0.97; df = 2, 72; P = 0.386; females, F = 2.62; df = 2, 67; P = 0.08; spring/summer: males, F = 8.31; df = 2, 97; P < 0.001; females, F = 7.04; df = 2, 87; P = 0.001.

mon among males. Of 54 parasitized females examined, only 5.6 % had more than a single egg, whereas 37.5 % of parasitized males (n = 122) bore 2-8 eggs attached to the body. Percent parasitism in general is also substantially higher in males. Total parasitism in the capture-recapture study was 15.0 % for males (n = 300), and 8.6 % for females (n = 243). Despite the high incidence of attempted superparasitism, it should be noted that only one *T. pennipes* larva ultimately emerged from each *L. phyllopus* caged in the laboratory. However, four larvae emerged from a single individual of *A. femorata* bearing 21 eggs.

Rearing experiments. Originally, only field rearing experiments were planned. However, both tulle cages and the enclosed bugs were subject to severe depredations from biotic and abiotic factors. Plants bearing cages collapsed during storms, drowning bugs in puddles, while high winds caused tulle cages to catch on thorns and rip open. Although the fabric appeared to provide adequate protection from chewing predators, salticid spiders and reduviids stalked the outside surface of the net bags. Unwary experimental nymphs traversing the inside mesh surface were captured through the netting by these predators, and sucked dry. Dead bugs were dismantled rapidly by scavenging ants, so that condition of corpses could not be used to distinguish death by predation from actual treatment effects. Therefore, survivorship was only analyzed in the laboratory trials.

Survivorship on vegetative tissue of *G. parviflora*, *H. annuus*, *H. latifolia*, and *S. altissima* was zero. Individuals caged on buds of these species fared marginally better, with overall survivorship of 4, 8, 8, and 20 %, respectively, but insufficient data were generated for statistical comparisons, either among plant species or between plant developmental stages. Bugs survived in adequate numbers for analysis only on reproductive stage treatments in field (40-65 %) and laboratory (55-70 %) trials.

Field cage experiments in 1977 showed that fifth instars could develop equally well on the various autumn host plants, all of

Table 4: Development of fifth-instar *L. phyllopus* caged on detached fruits and seed heads of various host plants in the laboratory, Austin, Texas, August 1978.

Plant species	Family	n	Growth increment (mm)[a]	n	Instar duration (days)[a]	n	No. of surviving nymphs[a]
Callicarpa americana	Lamiaceae	13	3.00 ± 0.68b	13	15.00 ± 3.98b	4	3.25 ± 1.71a
Campsis radicans	Bignoniaceae	14	3.46 ± 1.01b	14	22.57 ± 5.64a	4	3.50 ± 1.29a
Gaura parviflora	Onagraceae	19	3.24 ± 0.87b	19	10.84 ± 2.16c	4	4.75 ± 0.50a
Solanum eleagnifolium	Solanaceae	11	3.36 ± 0.67b	11	12.82 ± 3.71bc	4	2.75 ± 2.06a
control	——-	13	4.73 ± 0.67a	13	8.9 ± 0.76d	4	3.00 ± 1.41a

[a]mean ± standard deviation; entries in a column followed by the same letter do not differ significantly (ANOVA and Fisher's LSD test or Kruskal-Wallis test; P > 0.05); Growth: F = 9.38; df = 4, 69; P < 0.001; instar duration: F = 27.26; df = 3, 56; P < 0.001; survivorship: H = 5.03, df = 4, P = 0.28)
[b]control treatment received laboratory rearing diet

which were in the family Asteraceae (Table 2). Neither growth increment nor instar duration differed among the four plant species tested. However, some differences were noted among spring/summer host plants in 1978 (Table 2). Bugs on thistle (Asteraceae) and lizard-tail (Onagraceae) did not differ in developmental parameters, but both grew significantly less than bugs provided laboratory diet (sunflower seeds) or those caged on cultivated sunflowers (Asteraceae). A similar trend was found for stadium duration, which was longer on wild hosts than on sunflower seed.

Mark-recapture data (see above) indicated that dispersal to the adult host plant was delayed until after the teneral stage; therefore, collection site of incompletely sclerotized adults is a reliable indicator of the nymphal host plant. Results of the field rearing experiments were substantiated when length of teneral adults from different host plants was compared (Table 3). No differences were found among either males or females develaoping on three different species of Asteraceae in autumn. Spring/summer hosts again differed in food quality, however; both males and females developing on cultivated plants (tomato and sunflower) were significantly larger than those maturing on the wild host (thistle).

In laboratory rearing experiments (Table 4), neither survivorship nor growth increment differed across host plants from four families, although bugs on all wild hosts grew significantly less than those on the control diet of sunflower seed and green beans. Duration of the fifth stadium was extremely variable, significantly extended on all wild hosts compared with the control, and varying among and within host plant treatments as well. The adult molt was delayed significantly when pods of trumpet creeper were provided as food, although the growth achieved and the numbers of surviving bugs were similar to those on other plants tested.

Laboratory choice tests. Experiments in which seed heads of two host plant species were presented in a 1:1 ratio demonstrated no significant differences in nymphal preference (sign test, n = 34, P > 0.05). Second instars preferred *H. latifolia* in 20 trials, *G. parviflora* in 14 trials, and exhibited no preference in 2 trials. In contrast, results of laboratory tests between buds and immature seed heads of *H. latifolia* showed an overwhelming and highly significant preference for seed heads (sign test, n = 30, P < 0.001), which were selected by second instars in 28 out of the 30 trials in which feeding occurred.

Histology. Stems, peduncles, and pedicels of tomato, thistle, and camphorweed, and immature reproductive structures of beans and tomatoes, could be successfully preserved and sectioned; neither buds nor seedheads of Asteraceae were amenable to histological technique. Typical tracks, or stylet sheaths, of *E. galeator* and *L. phyllopus* are shown in Figure 5. Irrespective of plant part, both species produced sheath deposits externally in addition to lining the full pathway of the stylets with gelling saliva. MILES (1958) showed that maxillary and mandibular stylets of Heteroptera move in concert, so that (unlike some Auchenorrhyncha) the termination of the stylet sheath in a feeding probe is indicative of the target tissue. Adults of *E. galeator* feeding on stem tissue (including peduncles and pedicels) typically produced branching sheaths which caused massive destruction to the entire region of vascular tissue. Of 39 *E.*

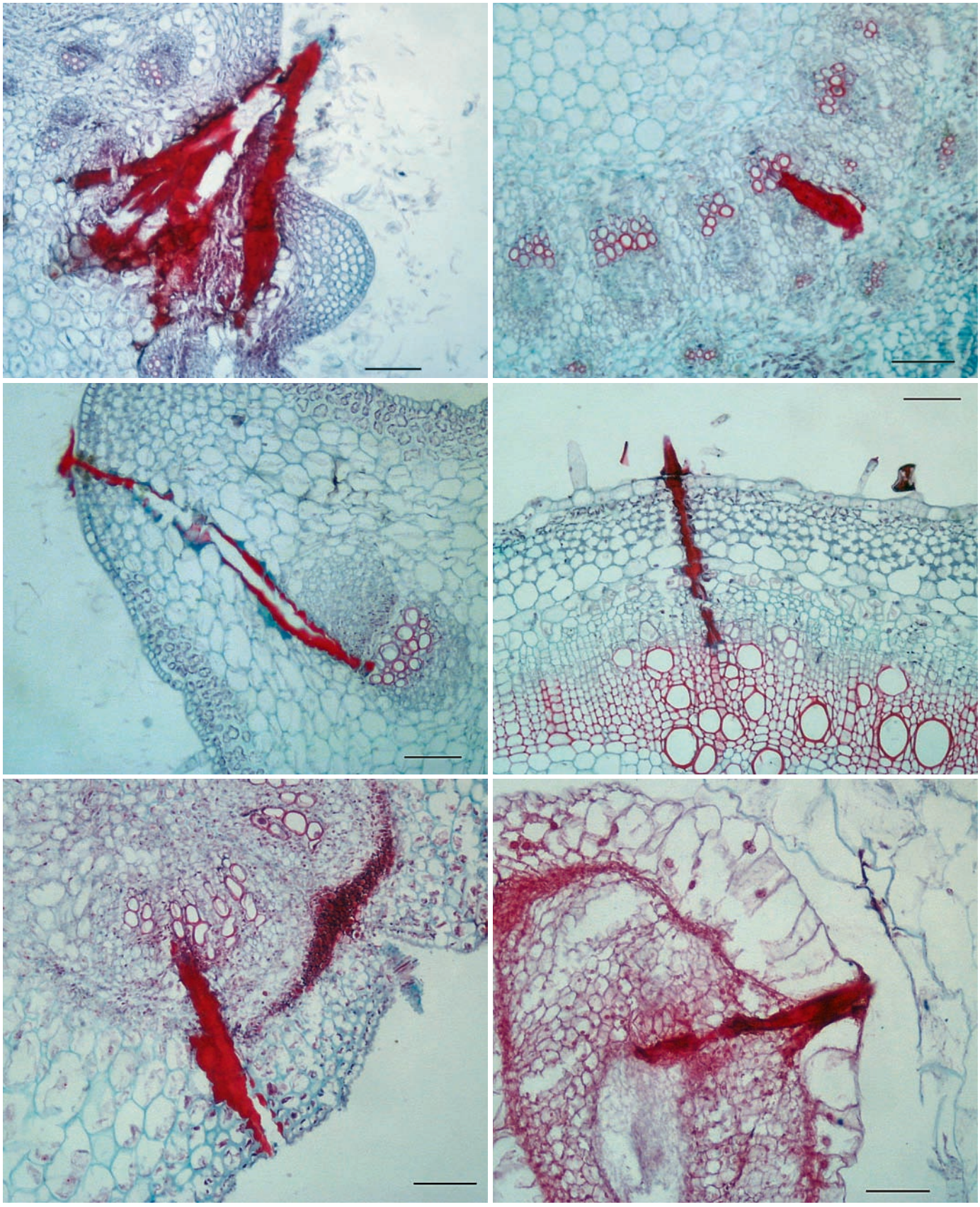


Fig. 5: Stylet tracks of coreids feeding on various hosts, photographed at 100x magnification, with horizontal bar indicating 100 µm; clockwise from upper left: *Euthochtha galeator* adult on peduncle of *Cirsium texanum*; *Leptoglossus phyllopus* adult on peduncle of *C. texanum* (partial track); *L. phyllopus* third instar on stem of *Lycopersicon esculentum*; *L. phyllopus* third instar on *L. esculentum* green fruit; *L. phyllopus* fifth instar on green pod of *Phaseolus vulgaris*; *L. phyllopus* adult on midvein of *C. texanum* leaflet.

galeator stylet sheaths examined, 22 were branched. Not all tracks could be followed with certainty because of damage or loss of serial sections; however, 19 of 24 that were confirmed to reach the vascular tissue were branched. Although *L. phyllopus* adults did occasionally insert their stylets into non-reproductive tissue such as leaves, pedicels, and peduncles, the target tissue in this case appeared to be primarily xylem, and the tracks rarely branched (Fig. 5). Branched tracks occurred in fruit and bud tissue and developing seeds (Fig. 5), but never to the extent observed with *E. galeator*. For *L. phyllopus*, 38 sheaths were located. In stems, only 1 sheath of 16 that reached vascular tissue was branched; 8 of these terminated in xylem and the remainder could not be definitively traced. In fruit and pods, most stylet sheaths penetrated to developing seed, although xylem was also targeted (Fig. 5). Penetration to pith was observed infrequently in both species.

Discussion

Leptoglossus phyllopus may be characterized as genuinely polyphagous, in the sense that individuals are capable of using a variety of host plant species. Not only is the overall set of host plants extensive across the geographic range (MITCHELL 2000), but bugs are local generalists as well. Fifteen species from seven families were used as breeding hosts at Brackenridge Field Station. Asteraceae predominated among host plants in the study, but this family is the second largest at the field site so the apparent preference may simply reflect availability.

Host-switching, or dispersal to an alternate host, may occur during three stages of bug development: nymph, teneral adult, or mature adult. Nymphal dispersal in the field could not be examined through mark-release studies. However, second instars (the stage that disperses from the egg mass to the breeding host) showed no preference between Onagraceae and Asteraceae in laboratory choice tests. In field studies, marked teneral individuals dispersed from the nymphal breeding host to an adult host plant belonging to a different family (e.g., Asteraceae to Solanaceae). Some post-teneral adults also moved among hosts and appeared to cross taxonomic lines between plant species readily. The long adult life span of *L. phyllopus* (up to 51 days adult residence in the mark-recapture study) may necessitate dispersal among plants with overlapping life cycles (i.e., from a senescing host plant to an alternate host in suitable condition); the same is true for teneral adults leaving the nymphal host. However, after the initial dispersal, the majority of recaptured individuals remained in a single patch of plants, or moved among patches of a single host species. Therefore, the most appropriate description of *L. phyllopus* feeding behavior is sequential (rather than concurrent) polyphagy. Diet mixing did occur, but it was infrequently observed. This accords with the conclusion of BERNAYS & MINKENBERG (1997), who found that under experimental conditions, mixtures of available host plants offered no significant advantage over single species for two polyphagous heteropterans, the pentatomid *Thyanta custator* (F.) and the mirid *Lygus hesperus* KNIGHT. These authors argue that for Heteroptera, unlike Orthoptera, the advantage of a generalist feeding strategy is versatility and greater resource availability rather than nutritional enhancement or dilution of allelochemicals.

In rearing experiments, fifth instars from the same cohort developed equally well on different species of Asteraceae. Even across plant families (Onagraceae, Lamiaceae, Bignoniaceae, Solanaceae), nymphal survivorship and growth were equivalent, although stadium duration was significantly extended on a few host species. The most extreme differences in fifth instar development occurred not among plant families, but between cultivated and wild hosts, suggesting that nutritional and host quality considerations, rather than plant taxonomy (and associated plant secondary chemistry), ultimately determine host plant selection. The importance of nutrient availability is underscored by the failure of caged insects to survive on vegetative hosts, and the significantly lowered survivorship on buds compared with immature seed heads and fruits. Preference experiments and distribution of bugs in the field corroborated the rearing experiments. Immature seed heads and fruits were used far out of proportion to

their availability; other plant parts were underused or avoided entirely.

The close correspondence of plant reproduction and *L. phyllopus* colonization indicates that patterns of host plant utilization are to a great extent determined by plant phenology. Bugs disperse between host plants with overlapping life cycles, as one species reaches senescence and the next species begins fruiting. Generations are continuous throughout the season, with reproductive diapause occurring only during the winter months. Thus, for *L. phyllopus*, dependence on relatively ephemeral plant fruiting structures necessitates periodic dispersal. The risks entailed in such host switching are reduced as the range of acceptable plant species increases. Polyphagy provides versatility and greater resource availability (BERNAYS & MINKENBERG 1997) but is tied to specialization on nutrient-rich reproductive tissue.

Clearly, *L. phyllopus* are specialists on plant structures, although not on plant species or families. Analogous feeding preferences have been documented for two heteropteran cotton pests. Bolls 7-27 days old are damaged by *Euschistus servus* (SAY) to a significantly greater extent in the field than are other boll ages (WILLRICH SIEBERT et al. 2005) whereas cotton buds (squares) are used preferentially by adults and older nymphs of the highly polyphagous *L. hesperus*. In the case of these lygus bugs, the target tissue is the anther sac; younger nymphs, whose stylets cannot reach the anther sacs of larger squares, are not economically damaging (ZINK & ROSENHEIM 2005). *Lygus lineolaris* also primarily damages developing anthers and staminal columns in cotton floral buds (WILLIAMS III & TUGWELL 2000).

Selection by *L. phyllopus* of feeding sites at the plant organ and tissue level differs from feeding behavior of lygus bugs and that of most other pentatomomorphan species studied. Mirid feeding creates lesions consisting of areas of plant tissue from which cell contents have been removed, sometimes distant from the termination point of the stylets (MILES 1987). Mirids and other Cimicomorpha do not produce a continuous stylet sheath; their extra-oral digestion via injected salivary enzymes (pectinase) is characterized as "macerate and flush" (or "lacerate and flush" by earlier authors, before the role of salivary enzymes was fully appreciated) (MILES & TAYLOR 1994; SHACKEL et al. 2005; ZENG & COHEN 2001). Pentatomomorphan bugs produce stylet sheaths when feeding on stem tissue, but exudation of sheath material does not accompany the full length insertion of the stylets into seeds (MILES 1959). Thus, these insects were originally described as either "lacerate and flush" feeders (on seeds) or "stylet sheath" feeders (on growing plant tissues) (MILES 1972).

Sheaths produced by milkweed bugs (MILES 1959) and chinch bugs (PAINTER 1928) feeding on stems are extensively branched at the level of the phloem, resembling the feeding by *E. galeator* in this study. Squash bugs deposit gelling saliva in all stem tissues, including collenchyma, parenchyma, phloem, and xylem (NEAL 1993). Wilting has been attributed to extensive blockage of xylem by saliva of *A. tristis* on squash and the pentatomid *Palomena angulosa* MOTSCHULSKY on potato (HORI et al. 1984, NEAL 1993). *Palomena angulosa* fed preferentially on leaves and petioles and inserted the stylets mainly to the phloem (HORI et al. 1984), but nymphs also fed on buds, destroying the tapetum and consuming pollen. In contrast, *L. phyllopus* feeding on stems and peduncles most frequently penetrate directly to xylem, with no branching and minimal destruction of vascular tissue. This behavior, coupled with the failure of nymphs to develop on vegetative tissue, strongly suggests that stem "feeding" in this species is essentially drinking from xylem. Xylem drinking by heteropterans was first noted by PAINTER (1928) in chinch bugs (Blissidae). These insects produce branching stylet tracks that pass intracellularly through leaf tissue of sorghum to the phloem, and often one branch terminates in xylem; PAINTER (1928) suggested that the xylem may provide "an extra source of water...especially during dry periods." WHEELER (2001) summarized observations of mirid stylet tracks in vascular tissue, and speculated that these insects may use xylem similarly.

Actual feeding (i.e., nutrient ingestion) in *L. phyllopus* occurs on reproductive tissue. In immature pods and fruit, a complete

stylet sheath is produced through the wall to the developing seed. This is similar to feeding by other *Leptoglossus* species. Nymphs of *Leptoglossus corculus* (SAY) feed on nucellar tissue of pine ovules in conelets (DEBARR & KORMANIK 1975); *Leptoglossus occidentalis* HEIDEMANN destroys the nucellus and disorganizes the female gametophyte of immature pine seeds (KRUGMAN & KOERBER 1969). Feeding by the latter species on developing and mature seeds of Douglas-fir causes depletion of protein and lipid reserves from storage parenchyma and reduces seedling emergence (BATES et al. 2000, 2001). Interestingly, examination of damaged seed and insect saliva suggests that neither lacerate-and-flush nor osmotic pump mechanisms are involved, and a mirid-like pectinase mechanism is suggested (BATES et al. 2000). Three species of Australian stem- or shoot-feeding coreids, *Mictis profana* (F.), *Amblypeta* sp., and *Amorbus* sp., have been shown to produce salivary sucrases to osmotically draw parenchyma cell contents into intercellular spaces ("osmotic pump"). These insects typically made short, unbranched, stylet sheaths (MILES 1987; MILES & TAYLOR 1994; TAYLOR & MILES 1994), unlike the branched tracks of stem feeders described previously, and they induce lesion formation and wilting of shoots beyond the point of feeding. It appears that coreid feeding may not fall neatly into a single category, but could include osmotic pump, lacerate-and-flush, and macerate-and flush strategies in different species. Understanding the mode of feeding is important, because the extent to which tissue is damaged by feeding, and the secondary chemicals released by such damage, could in turn affect diet breadth. For example, cyanogenesis in cassava roots is caused by cell wall rupture by the stylets of a polyphagous cydnid, thereby deterring feeding (RIIS et al. 2003). The influence of plant defensive chemicals on feeding behavior of Heteroptera and other piercing-sucking insects deserves further study.

Acknowledgments

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Zusammenfassung

Die polyphage Art *Leptoglossus phyllopus* (L.) wurde hinsichtlich ihrer Nahrungspflanzenpräferenz, (Wirtspflanzen)Gewebespezifität, ihres saisonalen Wirtspflanzenwechsels und ihrer Lebensgeschichte untersucht. Fang-Wiederfang, Zensus und Zuchtexperimente zeigten, dass sich diese Art polyphag ernährt, in dem Sinne, dass einzelne Tiere an Pflanzen unterschiedlicher Familien saugen. Entwicklungsparameter wie Körpergröße der Entwicklungsstadien und Überlebensrate unterscheiden sich nicht zwischen Wirtspflanzen verschiedener Familien; signifikante Unterschiede wurden jedoch zwischen unterschiedlichen Qualitäten der Nahrungspflanzen (z.B. wild vs. kultiviert) festgestellt. Die Dauer der Entwicklungsstadien unterscheidet sich bei verschiedenen Nahrungspflanzen im Experiment. Eine Spezialisierung an bestimmte reproduktive Teile der Wirtspflanzen, gekoppelt mit sequentieller Polyphagie und der Ausbreitung an bestimmte Wirtspflanzen über die Saison, erlaubt die Ausbildung mehrerer Generationen pro Jahr. Unterschiedliche Möglichkeiten der Nahrungsaufnahme und die Bevorzugung bestimmter Wirtspflanzengewebe bei Coreiden werden diskutiert.

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